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Research article

Determining the optimal movement strategies in environments with heterogeneously distributed resources and toxicants

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Environmental stress forces populations to move away from oppressive regions and look for desirable environments. Different species can respond to the same spatial distributions of resources and toxicants with distinct movement strategies. However, the optimal behavioral strategy may differ when resources and stressors occur simultaneously or if they are distributed in different patterns. We compared the total abundance of two strains of *Caenorhabditis elegans* with different locomotion speeds as they forage in various spatial distributions of resources and toxicants. Informed by the experimental observations, we proposed a new two-state population model, wherein nutrient uptake and reproduction are modeled separately, as driven by the spatial distribution of resources and toxicants. We found that fast movers had an advantage when either the toxicant coverage or the overlap between toxicants and resources was increased. Also, to assess the effectiveness of designing refuges to conserve species in stressful cases, we compared different preferences of locations of refuge areas according to movement strategies. Our mathematical model explained that fast movement enables individuals to consume resources at one location and reproduce at a separate location to avoid the toxicant-induced reduction in reproduction rate, which underlined its observed advantage in certain experimental settings. This work provided a better model to predict how species with different movement strategies respond to environmental stressors in natural systems.

Keywords: *Caenorhabditis elegans*, heterogeneous environment, optimal movement patterns, population abundance, refuge location, toxicant

Introduction

Movement is an important factor to consider in spatial ecology (Holt and Barfield 2001, Leibold et al. 2004, Jeltsch et al. 2013, Ōkubo and Levin 2013, Cantrell et al. 2020a), both for the long-term survival of metapopulations, and for designing

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effective management strategies for different species based on our knowledge of their movement patterns (Shew et al. 2012, Polic et al. 2014, Doherty et al. 2019). Natural populations exist in spatially heterogeneous environments where individuals move among a patchwork of habitats that vary in quality (Hastings 1983, Tilman and Kareiva 1997, Leibold et al. 2004, Clobert et al. 2012), e.g. animals move to find food, shelter, and mates, and to escape stressors such as contamination and predation (Araújo et al. 2020, 2022). A main question in spatial ecology is focused on understanding how patterns of movement on the individual level affect the dynamics on higher (population, ecosystem, and community) levels, especially in heterogeneous, patchy environments (Hastings et al. 2011). For instance, theory predicts that populations moving within heterogeneous environments reach higher total population size than their non-moving counterparts, and, paradoxically, higher size when the heterogeneous environment is replaced by an homogeneous environment (Skellam 1991, Holt and McPeek 1996, Dockery et al. 1998, Lou et al. 2016, Zhang et al. 2017). Such studies have important conservation implications, including understanding the impact of habitat fragmentation and loss, which are some of the greatest threats to biodiversity, on the resilience of the biological populations (Fahrig 2007, Alagador et al. 2014, Fletcher et al. 2018).

Theory from previous research proposed that there are two main types of movement: 'continuous movement' for less mobile species versus 'discrete stepping-stone movement' for more mobile species (Fahrig 2007, Alagador et al. 2012). It is suggested that, within a habitat containing several patches large enough to serve as home ranges, there are small changes in movement rates so that less mobile, continuous movement is advantageous. Alternatively, if those patches become too small due to habitat loss and fragmentation to maintain a viable population size, animals tend to increase movement rates to escape unsuitable habitats and gain access to more than one resource patch (Doherty et al. 2019). In addition to fragmentation that creates different patterns of habitat resources, other factors can change the suitability of an environment, leading to a change in movement strategy. One main threat to natural populations is environmental stressors, either as a natural part of the landscape, unintentional byproducts such as industrial pollutants, or resulting from intentional releases such as antibiotics and pesticides. Some populations respond to environmental stressors and toxicants by active avoidance, or by directing movement away, i.e. they move away from stressful regions in search of more desirable environments (Pearson and Dawson 2003, Godet et al. 2011, Meli et al. 2013), while others who stay can suffer from increased population mortality and declines in abundance (Huang and Wang 2022, Song et al. 2022), or respond with a combination of the two. To simplify the impact of toxicants in this study, we focused on the type of toxicant that mainly triggers an avoidance behavior of an organism instead of directly causing mortality.

Since the distribution patterns of stressors are usually heterogeneous in nature, it is critical to understand the impact of various distributions of stressors across both space and time (Purucker et al. 2007, Zhang et al. 2020). Some stressors start to invade suitable habitat patches and create smaller viable areas, such as when one contaminated stream flows into another and causes a progressive increase of toxicant coverage, which we describe hereafter as an 'invasion of stressors'. Alternatively, some stressors may be equal in size to the original habitat or resources, but depending on the initial location, they may have a different proportion of overlap with the resources. For instance, many nearshore environments and freshwater ecosystems have been suffering from increasingly severe anthropogenic disturbances, such as oil spills and urban runoff of metals (Johnston and Keough 2002, Allen et al. 2016, Burnett et al. 2021), and the original location of this pollution event determines how much the pollutant is overlapping with the habitat patch. Hereafter, we defined this case as an 'overlap between stressors and resources'.

It is critical to identify how the effects of heterogeneously distributed stressors and other contaminants vary among organisms with different characteristics (Purucker et al. 2007). Some well-studied factors that affect the ability of species and individuals to respond to and handle exposure to contaminants are damage-repair rate, age class, and the availability of food. One common response of organisms to stressors is by way of movement, which is determined both by organisms' inherent mobile ability, augmented by the need to use and exploit heterogeneously distributed resources (Webber et al. 2020, Zhang et al. 2020) and the potential avoidance of various groups of contaminants (Hallam and Lika 1997, Meli et al. 2013, Moreira-Santos et al. 2019). In many species, individuals adjust their movement based on the availability of foraging resources, such as by moving relatively slowly in environments with a clumped distribution of resources and moving relatively quickly in environments with a uniform distribution of resources (Webber et al. 2020). Understanding what movement strategies are optimal in different environments when both resources and stressors occur heterogeneously can help answer some critical questions in conservation (Palumbo et al. 2019); for example, the optimal design of a protection zone, or 'refuge', within which the population's continuous growth is guaranteed (Jin et al. 2023). Identifying responses of species with different (non-directed) movement speeds to different spatial configurations of refuges can provide insights into the way refuge locations might be designed to maintain the survival of target species. However, limited work has been done in this area (Bukola et al. 2015, Zanatta et al. 2020).

A body of theory, based on Lotka–Volterra-like equations (LV model), has been developed to predict how species with different movement strategies respond to spatio-temporally heterogeneous environments of resource distributions (Zhang et al. 2022). Recent studies have looked at the impact of heterogeneously distributed stressors to provide further theoretical predictions (Zhang et al.

2020). For instance, whenever toxicants are heterogeneously distributed between patches, a small amount of dispersal makes the consumer's total abundance larger than it would be without dispersal (Huang and Wang 2022, Song et al. 2022). A homogeneously contaminated environment is actually the least favorable habitat, and total abundance in these environments (with or without dispersal) is less than that under heterogeneous contamination with animal dispersal, with higher levels of heterogeneity corresponding to higher population growth rate and equilibrium size (Meli et al. 2013, Yu et al. 2023). Almost no theoretical studies have been performed to investigate the impacts of both resources and stressors, except a single state population model (Zhang et al. 2022), and we know of no experimental studies that have rigorously tested theoretical assumptions. Therefore, it is still unknown which movement strategies are best in environments with various patterns of resources and repelling toxicants, and whether it would be better for an organism to move into a patch with fewer resources with less stress or to a patch with higher levels of resources and stress.

The main objective of this study was to understand which movement strategies are more advantageous when toxicants are heterogeneously distributed in an ecosystem, using a combination of experiments and model simulations. Specifically, this study investigated how both the amount and arrangement of repelling toxicants and food resources within a landscape affect the population abundances of organisms with different movement strategies (slow versus fast) to identify the optimal movement strategies in different environments. To this end, we proposed three questions and hypotheses. First, what would happen if stressors were added over a greater area within a habitat that has a continuous patch of resources (case A: invasion of stressors)? We hypothesized that faster movers would initially have the advantage as toxicants were added, as they can escape the toxicants, but that the difference between slow and fast populations would begin to decrease the more toxicants were added and toxicity occurred regardless of escape ability. Second, if there are equal areas of stressors and resources, which movement strategy would be optimal as the overlap between stressors and resources increases (case B: overlap between stressors and resources)? We hypothesized that in environments with decreased overlap between resources and toxicants, slower movers could better utilize the uncontaminated resources by staying on the food, but in environments with increased overlap, faster movers would have an advantage by being able to uptake the contaminated resources and then reproducing at a separate location (avoiding toxicants). Finally, starting with a complete overlap between the stressors and original resources, what impact would an added refuge, or discrete patch of resources, have (case C: position of refuge)? We hypothesized that the distance of 'refuge areas' of uncontaminated resources from the contaminated resources would determine whether slow movers (nearby refuge) or fast movers (distant refuge) would have the advantage.

Material and methods

Experimental methods

Strains

Caenorhabditis elegans is a nematode worm species widely used as a model organism in biology, ecology, and toxicology (Anderson et al. 2004, Song et al. 2014, Ying Jiang 2016). The widespread use of this species is due to its low culture cost, short life cycle, fully sequenced genome, and the ease with which mass cultures can be generated (Song et al. 2014, Mashock et al. 2016). Two strains with random (e.g. with defects in directed) movement were used in this study – MIA471 *tax-2(p694) I*; *egl-4(n478) IV* and MIA472 *tax-2(p694) I*; *pdfr-1(ok3425) III* (Zhang et al. 2022). MIA471 is a 'roamer' strain that has a faster movement rate than MIA472, which is a 'dweller' strain. MIA471 diffused more quickly and evenly across the Petri dish, while MIA472 was more likely to remain and congregate in one area on the plate. Note that neither strain has directed movement toward resources because of the *tax-2(p694)* mutation (Dusenbery et al. 1975), which allowed us to focus on different diffusion rates on affected organisms' responses to environmental toxicants assuming no a priori knowledge of resource distribution. The non-directed movement of the strains used in this study means that while they were generally attracted by resources and repelled by toxicants, they had defects in both attraction and repulsion.

Culture environments of resources

Caenorhabditis elegans populations were maintained on normal growth media (NGM) circular plates (60 × 15 mm) seeded with 100 μl of OP50 *Escherichia coli*, cultured in B broth. Three to five L4 *C. elegans* were transferred to new plates every four days to maintain the population, i.e. to reproduce and develop enough new L4 stage worms for the experiments. Accordingly, we used *E. coli* to represent the resources of *C. elegans* populations during experimental trials. B broth was only used to seed the experimental agar plates if it was inoculated no more than two weeks prior to the seeding date, and to seed circular plates if it was inoculated no more than one month prior.

Toxicant environments

Copper acts as a neurotoxin to *C. elegans*, with even sublethal doses causing nerve damage and paralysis, reproductive capacity decrease, shortened life span, reduced food intake, and abnormal behavior. Worms exhibit a strong aversion to odorants they dislike, including copper and copper compounds, and begin avoiding lawns of bacteria with copper or copper oxide particles even at low concentrations, avoiding them completely at the highest particle levels (Munro et al. 2020, Parida 2022). Their copper avoidance is mediated through multiple neural pathways, including the ADL, ASE and ASH neurons (Sambongi et al. 1999). Copper sulfate ($CuSO_4$) is one of the most effective repellents of *C. elegans*, as both copper and sulfate ions are known to cause a chemotactic response in this species, and exposure to toxic levels of copper sulfate has been observed to reduce brood size and life span while slowing development (Govani et al. 2014, Mashock et al. 2016). We dissolved 1.25 g of copper sulfate pentahydrate ($CuSO_4 \times 5H_2O$, supplied by VWR International) in 500 ml of deionized water, creating a 0.01 M solution. This concentration was above the LC50 (0.88 mmol l^{-1}, or 0.0009 M) of copper sulfate pentahydrate for wild-type *C. elegans* in aqueous lethality tests, in which worms were added to 0.8 ml test solution in tissue culture plates for a 24-h exposure period (Song et al. 2014). Additionally, in our findings, this concentration resulted in a population size approximately 80% that of an environment without copper when the entire plate was covered with both food and toxicants (Supporting information). This level is above that demonstrated to be an effective repellent (Govani et al. 2014). This solution was then sterilized via autoclave (liquid cycle, 121°C, 45 min). To measure whether the copper would distribute across the Petri dishes over the trial period, we used X-ray fluorescence (XRF) to determine the copper concentrations in different areas of the plate after it was added (Supporting information). We found that while the copper did spread across the plate over time, the spread was limited to a modest and nonsignificant ~ 15% increase over 5 days, based on a plate half-covered in copper solution (Supporting information).

Heterogeneous environments of resources and toxicants

We used square Petri plates (100 × 100 mm) to design a variety of distributions of resources *E. coli* and toxicants ($CuSO_4 \times 5H_2O$). Each plate had a grid of six columns (1–6) and six rows (A–F). We divided each column into 'top' and 'bottom' halves (between rows C and D) for the purposes of counting – therefore, there were twelve separate sections on each Petri dish. We first dipped different sizes of 3D-printed blocks into B broth with *E. coli*, shook off any excess liquid, and placed the blocks on specific columns or rows on the square Petri dish, selected based on the environment we intended to create. Then, 2 days after the plates were seeded with *E. coli*, we added copper to the Petri dish to mimic environmental toxicants. As with adding *E. coli*, we used 3D-printed blocks to lightly place copper sulfate solution on specific columns or rows as experiments needed. To prevent *E. coli* from being moved into columns it was not meant to be in, the copper was first placed on columns without resources, then on columns adjacent to resources, and finally on columns containing resources. After copper was added to all the plates, they were left untouched for at least 1 h so that the copper solution could adsorb and dry properly before worms were added. Each environment designed for each case below had five replicates.

Case A: invasion of stressors

We created environments with half of the plate (columns 4–6) covered with *E. coli* and with different amounts of copper sulfate – ranging from one column (in column 6) to five columns (in columns 2–6). Note that we only tested the condition with half of the environment covered by food because not every habitat location in the field is ideal to be utilized. The empty patches represented areas that are not harmful or dangerous but do not offer value to the organisms. We generated six environments for this case: 000111, 000113, 000133, 000333, 002333 and 022333 (Fig. 1A). We gave an ID number to each of the environments, where: '0' indicates an empty column (no addition), '1' indicates a column with only *E. coli* food resources, '2' indicates a column with only Cu^{2+} toxicants, and '3' indicates a column with both *E. coli* food resources and Cu^{2+} toxicants. The last three

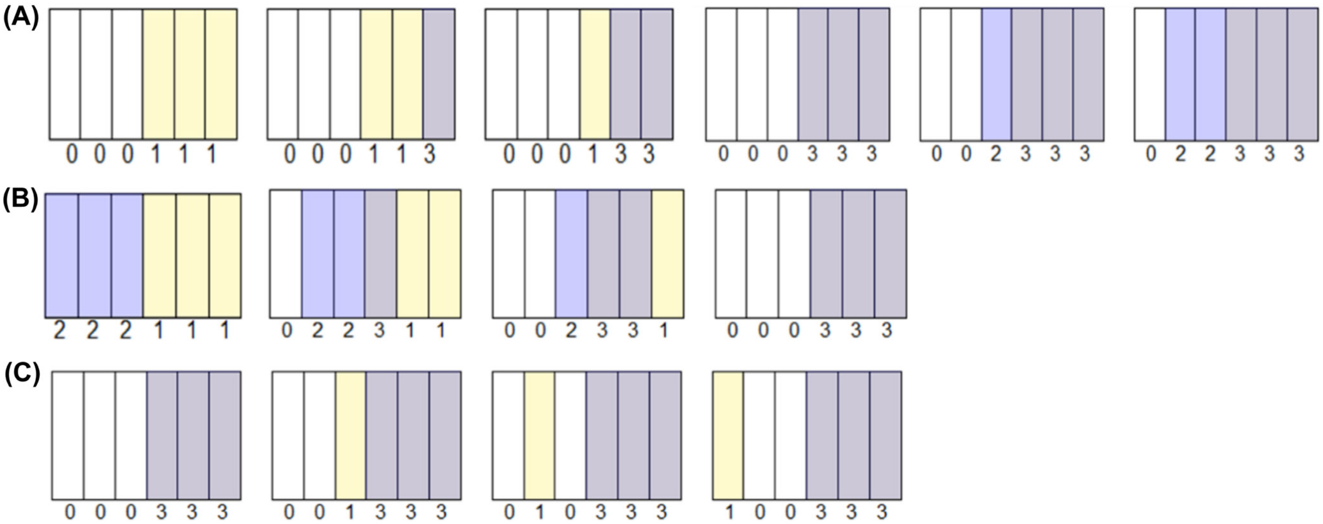

Figure 1. A diagram of the cases considered in this study. (A) Invasion of stressors – a progressive increase of toxicant coverage. (B) Overlap between stressors and resources – increasing the overlap of resources and stressors while keeping the total amounts constant. (C) Position of refuge – changing the distance of a 'refuge' area from a contaminated habitat. Yellow zones represent resources, blue represents toxicants, and gray represents areas with both resources and toxicants. '0' indicates an empty column (no addition), '1' indicates a column with only resources, '2' indicates a column with only toxicants, and '3' indicates a column with both resources and toxicants.

environments (000333, 002333 and 022333) tested whether adding more columns of toxicants would prevent faster movers from traveling from contaminated resources to a good or neutral habitat and therefore decrease their population.

Case B: overlap between stressors and resources

We created a gradient of overlap between resources and toxicants (0, 33, 67, and 100%) by changing the location of toxicants. For example, the 0% overlap (222111) was created by culturing *E. coli* on columns 4–6 while adding copper sulfate only to columns 1–3. Conversely, the 100% overlap condition (000333) was created by adding both the *E. coli* and copper sulfate to columns 4–6, leaving columns 1–3 empty (Fig. 1B).

Case C: position of refuge

We created three unique locations of refuge by changing the distance of a 'refuge' area (made of one column of *E. coli*) from the contaminated habitat (001333, 010333 and 100333) to ultimately compare to 000333 (Fig. 1C).

Population counting

Initially, three L4 worms were added at the center of each Petri dish (between rows C and D, and columns 3 and 4). All the experimental plates were kept in a 20°C incubator for approximately 120 h, the amount of time it takes for the majority of the worms to reach a size easily counted under a microscope (above L3 stage) before the food is depleted. After this time had passed, the experimental plates were moved into a refrigerator (4°C) for approximately 30 min to let the low temperature slow the movements of the worms, making them easier to count. The abundance of *C. elegans* (stage L3 and above) within each of the twelve sections was counted and recorded (n = 280).

Statistical analysis

The main and interactive effects of the environment and locomotion on the population abundance were analyzed by generalized linear regression models (GLM) for each case, and a negative binomial distribution was used to consider the overdispersion issue from analyzing count data. The assumptions of equal variance and normality were checked based on residual plots with fitted values and Q–Q plots, respectively. The above analyses were conducted by the 'MASS' package in the R environment (Ripley et al. 2013, www.r-project.org). Moreover, we made multiple comparisons of the population abundance between the combinations of different environments and locomotion. The multiple comparisons were based on the overall false discovery rate (FDR) method to control the proportion of falsely significant differences in the multiple comparisons (Verhoeven et al. 2005), and the FDR method was conducted by the 'emmeans' package in the R environment (Lenth and Lenth 2018). The distribution of the worms was analyzed with similar methods as described above, with 'column' as an additional predictor. We also considered the nested data structure caused by the fact that the six columns belonged to one environment.

Theoretical methods

In previous work, a single-state population model was used for modeling *C. elegans* population (Zhang et al. 2022). A typical model is given as follows:

$$\begin{cases} \dfrac{du_1}{dt} = \mu(u_2 - u_1) & t > 0, \\ \quad + \alpha_1 u_2 + b_1(1 - \sigma_1)u_1, & \\ \dfrac{du_i}{dt} = (\mu + \alpha_i)(u_{i+1} - u_i) & t > 0, \\ \quad + (\mu + \alpha_{i-1})(u_{i-1} - u_i) + b_i(1 - \sigma_i)u_i, & \\ \dfrac{du_N}{dt} = \mu(u_{N-1} - u_N) & t > 0, \\ \quad + \alpha_{N-1}u_{N-1} + b_N(1 - \sigma_N)u_N, & \\ u_i(0) = u_i^0 \ge 0, \not\equiv 0. & t > 0, \end{cases} \qquad \text{(model 1)}$$

where $u_i(t)$ denotes the number of worms on patch i, $i = 1,\ldots,N$. μ denotes diffusion rate across patches. α_i is the propensity of movement from patch $i+1$ to patch i and depends on the level of toxicants in adjacent patches. $b_i = br_i/(k_b + r_i)$, r_i and σ_i are the nutrient level and toxicant level in patch i, respectively, where b is the maximum birth rate and k_b is the half saturation constant. Indeed, it is a mathematical result that any model describing the growth of a randomly diffusing population in a spatially heterogeneous, but temporally constant, environment predicts that strains with low locomotion always exhibit a higher growth rate than those with high locomotion (Hastings 1983, Altenberg 2012), and the same holds when $\frac{\alpha_i}{\mu} \ll 1$. However, models such as (model 1) appear to be too simplistic as they fail to capture the experimental results where strains with high locomotion can sometimes have greater population abundance (Fig. 2–5). Indeed, an important assumption in (model 1) is that worms only reproduce on the food patches and cannot reproduce where nutrients are absent. This key assumption does not hold for the present experiment, as the worms move relatively fast and can lay eggs in patches where nutrients are absent. Indeed, it can be observed from the heatmap showing the distribution of worms with high locomotion that significant reproductive events occurred on the patches without nutrients (Supporting information). Therefore, the distribution of nutrients is not an accurate proxy for the average spatial reproductive rate of the individuals.

Informed by the experimental observations, we propose the following two-state population model, separating the process of nutrient uptake from the process of reproduction. Our new model is partly motivated by the adult–juvenile model introduced by Cantrell et al. (2020b), where the relative growth rate experienced by the adult and juvenile stages depends on spatial locations in different ways. To describe our new model, we suppose the spatial domain consists of N discrete, equal-sized patches, and categorize the population of *C. elegans* into $2N$ compartments $(u_1,\ldots,u_{\mathrm{N}},v_1,\ldots,v_N)$, where $u_i(t)$ and $v_i(t)$ denote the number of *C. elegans* in the i-th patch with, respectively, low and high food reserve. In the following, we only describe the rate of change of u_i (population with low food reserve), as those for v_i (population with high food reserve) can be similarly understood. Each individual moves between patches via diffusion with rate μ:

$$\text{Rate of change of } u_i \text{ due to diffusion}$$
$$= \mu\left(u_{i+1} - 2u_i + u_{i-1}\right).$$

While the movement of worms is indifferent towards nutrient levels, it can have certain avoidance of toxicants:

$$\text{Rate of change of } u_i \text{ due to toxicant gradient}$$
$$= \alpha_i\left(u_{i+1} - u_i\right) + \alpha_{i-1}\left(u_{i-1} - u_i\right)$$

where α_i is the propensity of movement from patch $i+1$ to patch i and depends on the level of toxicants in adjacent patches. The movements of v_i are modeled in the same way.

Moreover, each individual organism switches between the states with or without internal food reserves. Specifically, an individual switches from a low to a high reserve state in a food uptake event with rate r_i proportional to the nutrient availability, while it switches from high to low food reserve in the reproduction event with rate k, which is the same for all patches:

$$\text{Rate of change of } u_i \text{ due to exchange of states}$$
$$= -r_i u_i + k v_i.$$

$$\text{Rate of change of } v_i \text{ due to exchange of states}$$
$$= -r_i u_i - k v_i.$$

Finally, the birth event happens during the switching from high to low food reserve and leads to a corresponding increase in the number of u_i (individuals of low good reserve). For simplicity, we assume that newborns appear in the low food reserve state u_i, instead of including a juvenile stage in our model:

$$\text{Rate of change of } u_i \text{ due to birth of new members}$$
$$= kb\left(1 - \sigma_i\right)v_i$$

where k is as above, b is the maximum birth rate, and σ_i is the toxicant level in patch i. The reproduction (and consumption of food reserve) is possible in every patch, but the expected number of offspring (or reproduction rate) is spatially dependent and declines in the presence of toxicants. Putting these assumptions together, we obtain the following system of $2N$ differential equations:

$$\begin{cases} \dfrac{du_1}{dt} = \mu(u_2 - u_1) + \alpha_1 u_2 - r_1 u_1 \\ \quad + k v_1 + kb(1-\sigma_1)v_1 \\ \dfrac{du_i}{dt} = (\mu + \alpha_i)(u_{i+1} - u_i) \\ \quad + (\mu + \alpha_{i-1})(u_{i-1} - u_i) \\ \quad - r_i u_i + k v_i + kb(1-\sigma_i)v_i \\ \dfrac{du_N}{dt} = \mu(u_{N-1} - u_N) + \alpha_{N-1}u_{N-1} \\ \quad - r_N u_N + k v_N + kb(1-\sigma_N)v_N \\ \dfrac{dv_1}{dt} = \mu(v_2 - v_1) + \alpha_1 v_2 - r_1 u_1 + k v_1 \\ \dfrac{dv_i}{dt} = (\mu + \alpha_i)(v_{i+1} - v_i) \\ \quad + (\mu + \alpha_{i-1})(v_{i-1} - v_i) + r_i u_i - k v_i \\ \dfrac{dv_N}{dt} = \mu(v_{N-1} - v_N) \\ \quad + \alpha_{N-1}v_{N-1} - r_N u_N - k v_N. \end{cases} \qquad \text{(model 2)}$$

Assuming that the toxicant and resource levels remain temporally constant, the effective growth rate of the population can be estimated by the dominant eigenvalue λ of the multi-patch system wherein the time derivative $\dfrac{du_i}{dt}$ and $\dfrac{dv_i}{dt}$ in (model 2) are replaced by λu_i and λv_i, respectively (Vasilyeva and Lutscher 2012, Mierczyński 2014, Lam and Lou 2022). Such a dominant eigenvalue λ exists thanks to the Perron–Frobenius theorem (Perron 1907). Then, we use the expression $e^{\lambda T}$ to approximate the population abundance after time T, with $T=5$ days. With this mathematical model, we can compute the population abundance for strains with high/low locomotion in different environmental settings determined by the spatial distribution of resources and toxicants.

The assumptions on the movement and internal storage of nutrients are supported by the physiology of *C. elegans*. For simplicity, we assume that the toxicant and resource levels are independent of time (e.g. approximately constant during the time course of the experiment). See the Supporting information for the detailed mathematical model and further theoretical results. Our results were also further explained mathematically in Wang et al. (2024).

We estimated the parameters of models 1 and 2 and computed the expected population abundance under various nutrient/toxicant distributions that appeared in the experimental settings. Parameter values are listed in Table 1. Among them, our estimation of the parameters follows the principles below: 1) the models 1 and 2 are simple in the sense that the number of parameters is less than the data points obtained from empirical experiments. 2) The parameters are estimated to account for the order of magnitude of the total population abundance observed at the end of the experiment (Fig. 2–4A). In the case without toxicants, this number is also consistent with the brood size measurement in Zhang et al. (2022) (Supporting information). 3) Numerical results show the relative advantage of slow versus fast movers, and they do not change qualitatively as we vary parameters.

Results

Case A: invasion of stressors

In the experiments, adding more patches of toxicants to a continuous patch of resources led to a general decrease in population abundance of both slow and fast movers (Fig. 2A). In our control environment without toxicants (000111), there was no significant difference between fast and slow populations. In this environment, slow movers were mainly found in column four, with some spread into columns five and six. Fast movers, on the other hand, were more evenly spread throughout columns three through six (Supporting information). When one or two columns of toxicants were added (000113 and 000133), both populations decreased, though slow movers tended to decline more, albeit not significantly more in 000133. When toxicants covered the resource patches completely (000333), we found a significant decrease in the total abundance of the slow strain, whereas the fast strain also decreased in abundance but maintained a significantly higher population than slow movers. In 000333, the slow strain tended to cluster in columns where there were both resources and toxicants, while the fast strain was mostly counted in columns just outside the area of contaminated resources (Supporting information). The distribution of the worms was statistically significant ($p < 0.001$). The overall abundances of both strains decreased similarly in cases of 002333 and 022333 with more toxicant invasion to the entire area (apart from a small, nonsignificant increase in slow movers between 000333 and 002333). However, as more toxicants were added, the fast-moving strain declined more rapidly than the slow strain, and the difference between movement strategies became nonsignificant (Fig. 2A). The population model 2, where individuals can switch between two energy states, overall seems to capture the experimental outcome qualitatively and can better predict the winning (fast or slow) strain found in the empirical data in environments with more invasion or coverage of toxicants. Importantly, model 2 can capture the higher abundance of fast movers found in 000333 trials. We do notice, however, that when there were no toxicants (000111), the model predicted a higher abundance of slow movers than seen in the empirical results (Fig. 2B).

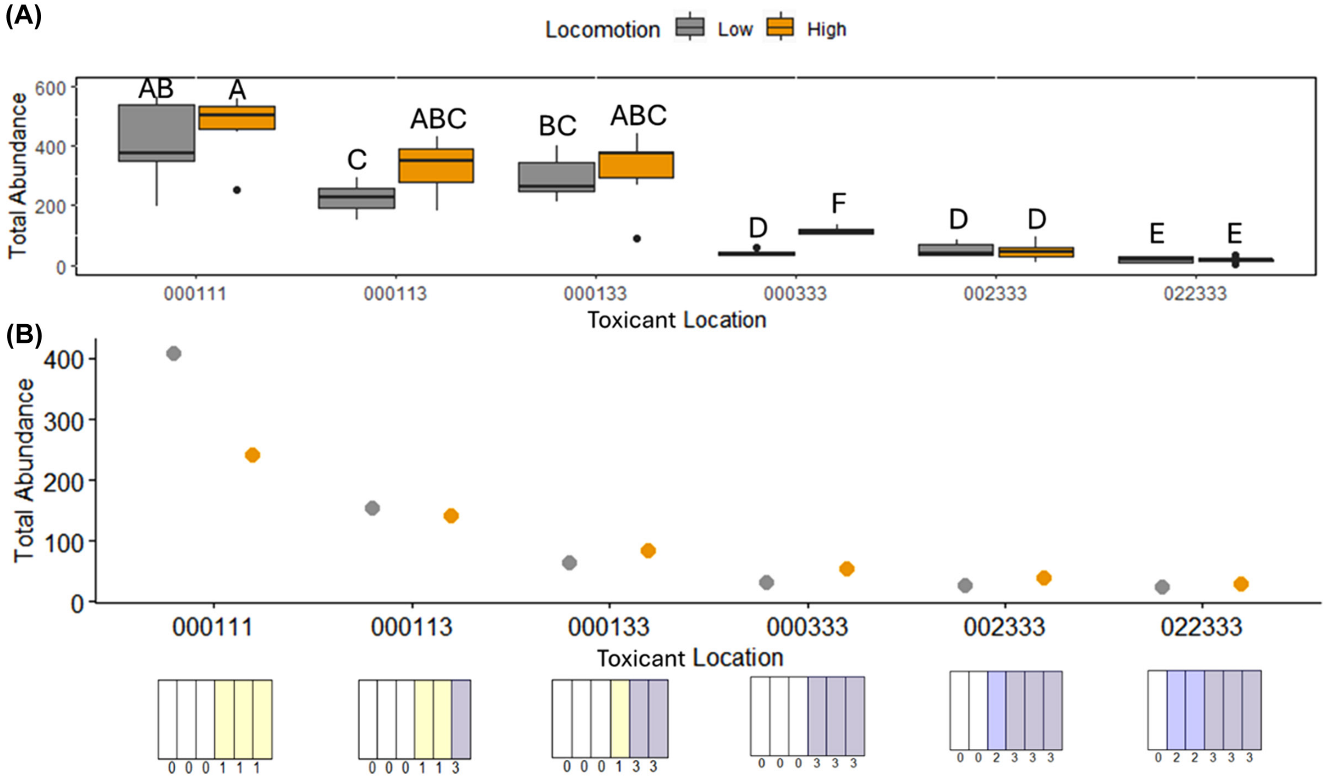

Figure 2. (A) Experimental population abundances of *Caenorhabditis elegans* strains (high and low locomotion) in environments 000111, 000113, 000133, 000333, 002333 and 022333. This figure shows the effect on populations during an invasion of stressors. Letters show significance between environments and locomotion. (B) The mathematically expected population abundance of *C. elegans* strains (with high or low locomotion) in environments 000111, 000113, 000133, 000333, 002333, 022333 (increasing amount of area covered by stressors). The numerical results are obtained from the two-state model 2.

Case B: overlap between stressors and resources

When toxicants were not completely overlapping with resources (222111, 022311 and 002331), the strain with lower locomotion tended to have a higher population abundance than the strain with higher locomotion, though the difference between strains was not significant (Fig. 3A). Both populations decreased in 002331 and 000333, though in the latter, the worms with higher locomotion speed showed a significantly larger abundance. The population of slow movers in 000333, where no area of resources was free from copper, was significantly different compared to the population of slow movers in all other test environments that had some level of resources that did not contain copper. Overall population abundance was lowest in 000333 and highest in 022311. We noticed both strains had similar clustering patterns when toxicants and resources had less overlap; in other words, when there was an area with only resources, both strains tended to gather there (Supporting information). The distribution of the worms was statistically significant ($p < 0.001$). The simulated differences in population abundance according to model 2 were consistent with our empirical data in this case among all the environments (Fig. 3B).

Case C: position of refuge

When a single column of resources was added to the environment of 000333, we noticed it had different impacts on slow and fast movers depending on its location. Environments with refuges had greater overall population abundances than 000333 (Fig. 4A). When the extra column was added next to the overlapping resources and toxicants (001333), slow movers had a slightly greater abundance than fast movers. When the column of resources moved farther away (010333 and 100333), fast movers benefitted more, with a significantly larger abundance in both environments. In 001333, slow movers gathered heavily in column three, the only section with uncontaminated food, with some individuals seen in columns two and four. However, fast movers mostly spread through columns one through three, with most individuals in column one. In 010333, slow movers distributed to column two (which contained the refuge area), column four, and column six, though in small amounts. Fast movers, on the other hand, were mostly found in columns one through three, with some individuals in columns four through six. We found that 100333 showed similar results, with fast movers still having great abundance in columns one through three and some individuals in other columns, while almost no slow-moving individuals left columns four through six (Supporting information). The distribution of the worms was statistically significant ($p < 0.001$). The simulated differences in population abundance according to model 2 were consistent with our empirical data in this case among all the environments (Fig. 4B).

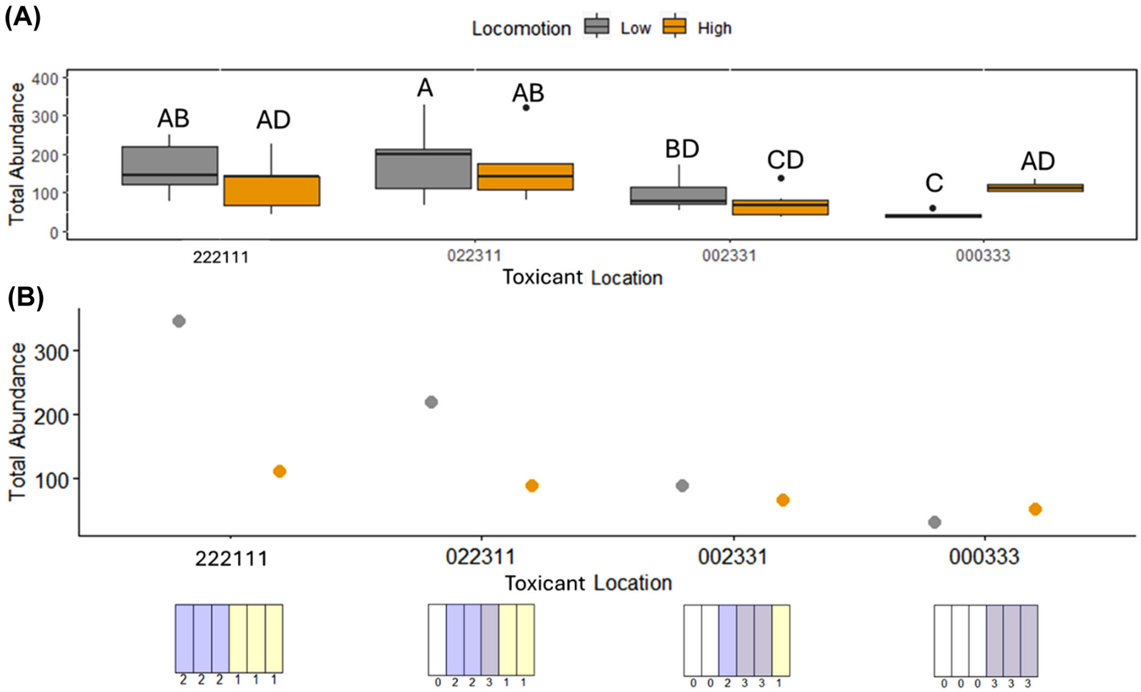

Figure 3. (A) Experimental population abundances of *Caenorhabditis elegans* strains (high and low locomotion) in environments from low to high overlap of toxicants and resources (222111, 022311, 002331, and 000333). Letters show significance between environments and locomotion. (B) The mathematically expected population abundance of *C. elegans* strains (with high or low locomotion) in environments 222111, 022311, 002331 and 000333 (varying degree of overlap between resources and toxicants). The numerical results are obtained from the two-state model 2.

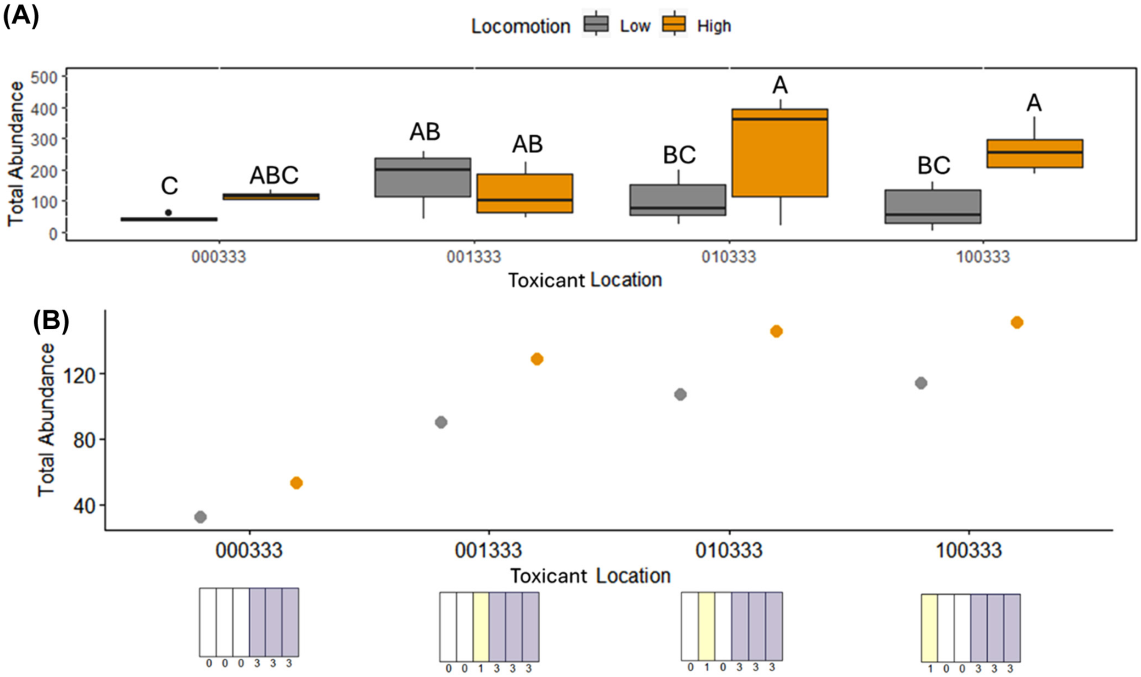

Figure 4. (A) Experimental population abundances of *Caenorhabditis elegans* strains (high and low locomotion) in environments 000333, 001333, 010333 and 100333, showing how the presence and position of a 'refuge' affected population abundance. Letters show significance between environments and locomotion. (B) The mathematically expected population abundance of *C. elegans* strains (with high or low locomotion) in environments 000333, 001333, 010333 and 100333 (with varying distance from refuge). The numerical results are obtained from the two-state model 2.

Comparison of the mathematical results simulated by the two models

To facilitate the comparison of the mathematical results simulated by the two models, we calculated the population abundance proportions of the strains under two locomotion speeds (fast and slow) and plotted them in Fig. 5. Here, the population abundance proportion is defined as the population abundance of the slow-moving strain divided by the total population abundances of both the slow-moving and fast-moving strains. Therefore, data above the horizontal black line at 0.5 indicate that the slow-moving strains win; and, conversely, data below the black line indicate that the fast-moving strains win. The numerical results show that in the single state model 1), the slow movers always win in every environment (Fig. 5). In contrast, the two-state model 2 was able to predict the winning (fast or slow) strain in most environments. The two-state model 2 where individuals can switch between two energy states seems to capture the experimental outcome qualitatively.

Assuming that the dispersal rate μ is not small (which is the case for *C. elegans*), we derived sufficient conditions for

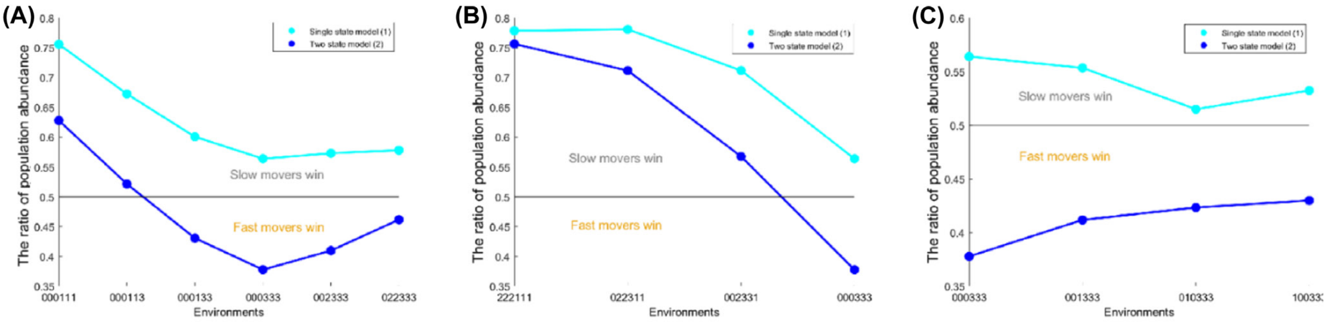

Figure 5. (A) The mathematically expected population abundance proportions of *Caenorhabditis elegans* strains (low locomotion: high and low locomotion) in environments 000111, 000113, 000133, 000333, 002333 and 022333. (B) The mathematically expected population abundance proportions of *C. elegans* strains (low locomotion: high and low locomotion) in environments 222111, 022311, 002331, and 000333. (C) The mathematically expected population abundance proportions of *C. elegans* strains (low locomotion: high and low locomotion) in environments 000333, 001333, 010333 and 100333. All numerical results are obtained from models 1 and 2.

Table 1. Parameters used in models (1) and (2). Some parameters are based on the current and previous experimental data, such as *N*, *T*, *b*, k_h and k (Zhang et al. 2022, Supporting information). Other parameters, such as r_i, σ_i and μ, are educated guesses where the order of magnitude lies in reasonable ranges based on empirical data. The numerical results are not sensitive to small changes in these parameters.

Parameter	Default value	Description
r_i	With resource = 2.7, without resource = 0	Resource level in patch *i*
σ_i	With toxicant = 0.5, without toxicant = 0	Toxicant level in patch *i*
μ	High diffusion rate = 30, low diffusion rate = 5	Diffusion rate
α_i	$\sigma i_{+1} - \sigma_i$	Directed movement rate
b	2	Maximum birth rate
k_h	1	Half-saturation coefficient
k	1.8	Reproductive event rate
N	6	Number of patches
T	5 days	Experiment time

the distribution of toxicants and resources so that the faster (or in some cases, slower) strain has higher effective growth rate, and hence higher terminal population abundance (Supporting information). See Fig. 6 for the dependence of the effective growth rate with respect to the motility rate μ in different environments. We also refer to the Supporting information for additional theoretical results justifying the monotone dependence on μ Our result gave a mechanistic explanation of the higher population abundance observed in strains with higher motility when the distributions of toxicants and resources are completely overlapping (the environment 000333), and that higher population abundance is observed in strains with lower motility when the toxicants and resources are distributed in separate patches (the environment 222111; Supporting information).

Discussion

Even relatively small changes in stressors can cause relatively abrupt and extensive changes in ecosystems; hence, understanding the biological response to increasing anthropogenic stressors is an important factor to consider when evaluating the well-being of an ecosystem (Allen et al. 2016, Burnett et al. 2021), and how that influences organisms with different movement strategies. Knowledge of animal movement provides important insights into the ecology of individuals, populations, and ecosystems (Hastings 1983, Tilman et al. 1997, Hanski 1998, Holt and Barfield 2001, Leibold et al. 2004, Boback et al. 2022). When toxicants or pollutants are introduced into the environment, it is important to identify how they select for the optimal movement strategy, including overlapping distributions of toxicants and resources, and the creation of a toxic barrier between contaminated and uncontaminated (good or neutral) habitats. A better understanding of the selective forces imposed by the joint distribution of resources and toxicants will ultimately inform us which organisms are most threatened in different situations, as well as the best course of mitigation, such as the effective design of refuge location.

The results of our first case (invasion of stressors) showed that the strains with low versus high locomotion speeds had generally similar responses to a continuous invasion of stressors, and population abundance generally decreased with the addition of stressors. Previous studies have found that the addition of environmental stressors caused lower abundance, and toxicant treatment-related responses of macroinvertebrate populations were more severe when a larger surface area of habitat was covered by toxicants (Brock et al. 2010, Muhling et al. 2012, Willson and Hopkins 2013, Hazen et al. 2016). However, one important and new result we showed is that when resources and repelling toxicants are completely overlapping (000333), the fast strain had a significantly higher abundance than the slow strain. Our results suggest a new perspective that organisms with a faster movement rate can take advantage of the empty, neutral areas to escape from the stressors, which will help them sustain a relatively higher population abundance when compared with slower-moving strains. A similar phenomenon has been shown in a natural aquatic system after the 2010 Deepwater Horizon oil spill impacted a portion of the spawning habitat of Atlantic bluefin tuna during their spring spawning season. A prior study found that adult bluefin tuna can move at a rate of approximately 100 km per week, allowing them to move and avoid direct exposure to oil for prolonged periods to maintain higher abundances of larvae in the remaining unaffected areas (Muhling et al. 2012, Hazen et al. 2016). Furthermore, when more columns of repelling toxicants were added to 000333, we found that, while populations of both slow and faster movers declined, faster movers declined at a greater rate and lost their prior advantage of escape in 000333, which supported our first hypothesis. These results could address a current major concern in ecology, the management of invasive species, and the copper compound that was added to the experimental plates could be viewed as a barrier to prevent exotic species spread (Goetz et al. 2021). Given that invasive species have a significantly higher dispersal rate than native species (Sih et al. 2004, Zhang et al. 2023), and most areas treated with chemicals often face re-invasion by the original pest or other unwanted exotic species (Blackie et al. 2014, Zhao et al. 2020), our results emphasized the importance of the size of barriers to block an invasion (Almeida et al. 2024). Enough areas that are detrimental to the fast mover are required to limit their ability to escape from the contaminated area and reach a neutral habitat and suppress those populations in relatively low densities (Almeida et al. 2024).

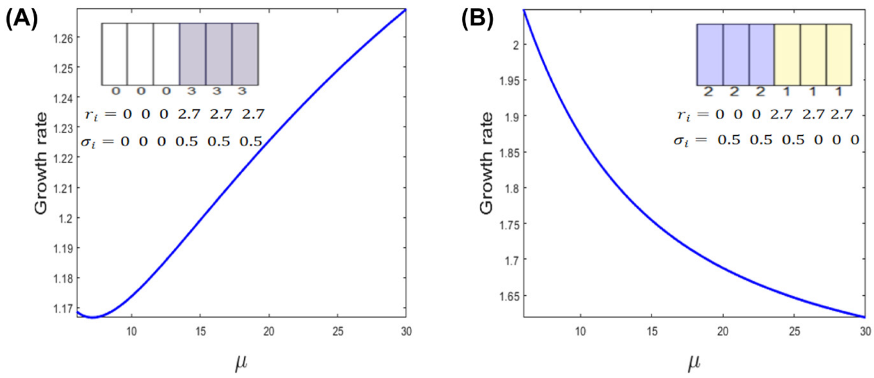

Figure 6. (A) Population growth rate of *Caenorhabditis elegans* with respect to μ in environment 000333, showing how the growth rate of population varies with dispersal rate μ. (B) Population growth rate of *C. elegans* with respect to μ in environment 222111.

Our second case (overlap between toxicants and resources) tested four levels of overlap between resources and repelling toxicants (0, 33, 67 and 100%) while keeping the total area of toxicants the same. Although there was no significant difference between the two strains, we did notice a higher population abundance of the slow strain in environments with more columns of uncontaminated resources, suggesting the importance of having at least a single column with resources to provide 'safe areas' for the slow strain. This supported our second hypothesis, and our results hence supported a conservation idea that local uncontaminated breeding sites might export enough recruits that overall impacts of a contaminated site are minimal (Rowe et al. 2001), especially in the case of species with lower movement rates. Alternatively, fast movers did better only with 100% overlap due to their ability to escape from the stressors. Indeed, the probability of leaving a protected site to obtain more resources, as when there was fast movement, depends on the tradeoff between the risk and benefits of leaving. The main benefits of movement are to avoid intra-specific competition, particularly kin-competition, in the current site, and to take advantage of under-exploited sites elsewhere (Fahrig 2007). But if the risks outweigh the benefits of leaving, slow movement, or staying in a location, becomes an optimal strategy. Previous studies have also compared the effectiveness of adding chemical barriers when treating invasive *Aedes albopictus* mosquitoes, which do not disperse far from their larval habitat. The study showed that insecticides were more effective when not just applied to their larval containers, but as barriers in the surrounding habitat (Faraji and Unlu 2016). Similarly, New Zealand mud snails, known for rapid movement and invasion of aquaculture facilities, can avoid copper-treated surfaces and continue to travel along uncontaminated paths – but when an entire surface is covered with toxicants to create a barrier, they quickly become stationary, only moving a short distance before becoming permanently immobile (Myrick and Conlin 2011).

Refuges are important to conservation management because of their potential to protect species from difficult-to-manage threats. Setting aside protected areas of land is a simple, but ubiquitous, approach for the conservation of biodiversity (Dobson et al. 1997, Selwood and Zimmer 2020). Our study found a new perspective that, when the same size of refuge area is added to the system, organisms with different locomotion speeds benefit differently depending on where the refuge is placed. Specifically, slow-moving organisms benefit more if the refuge is close to their contaminated habitat, while fast-moving organisms benefit more as the refuge is moved farther away, supporting our third and final hypothesis. Just as contamination of habitat can reduce the ability of populations to supplement nearby sinks, creation of uncontaminated habitat can increase the viability of nearby populations in contaminated habitats (Willson and Hopkins 2013). The decision as to which habitat should be restored may be just as important as to how much is to be restored, and refuges should be a part of interconnected ecosystems that biota are able to retreat to during adverse conditions. However, few conservation management plans take spatial effects and connectivity into account (Huxel and Hastings 1999, Selwood and Zimmer 2020). Our results suggest that conservation managers should consider the locomotion of the species of interest in refuge planning, as it is crucial that it is set in a location that would most benefit that species. For example, as extinction often occurs first for less mobile species, the natural habitat of such species should be identified so that restored patches can be placed relatively nearby to ensure survival of these slower-moving species (Huxel and Hastings 1999).

This study also provided new theoretical insights on the evolution of dispersal, as we developed a model to better capture our experimental data that can be applied to other systems to produce more varied predictions. Previous models with a single-state structure of *C. elegans* (Zhang et al. 2022) consistently predicted that slow-moving strains exhibited higher growth rate or population abundance compared to those with fast-moving strains, as with random movement, faster individuals were more likely to move from favorable to unfavorable conditions than the slower movers, thus creating a greater mismatch to the resource distribution. However, in our experimental setting when resources and toxicants follow different distributions, the optimal distribution can be different depending on the state of the individual. It is optimal to follow the resources if nutrient uptake is critical, while it is optimal to avoid toxicants to maximize expected number of offspring. To overcome the simplifications of the previous model and better explain the current experimental results, we argued that it is critical to incorporate more experimentally observed details into the modeling process, and introduced a state-switching model that accounts for two levels of internal food reserve, where nutrient uptake and reproduction are separate processes and are affected by the distributions of nutrients and toxicants in different ways.

Ecological models of animal movement involving state-switching are increasingly recognized by researchers (Fagan et al. 2019, Cantrell et al. 2020b, 2023). In many studies, it is recognized that animals do switch between different movement modes, and models incorporating switching states are necessary to analyze movement data (Patterson et al. 2008, McClintock et al. 2012). While incorporating such context dependence in mathematical models entails a substantial increase in complexity, it offers opportunity to more fully integrate key biological features. Our mathematical model showed that state-switching alone (without toxicant avoidance) is enough to account for the reversal of relative advantages of slow versus fast diffusers in the experiments. For instance, consistent with the experimental results, our mathematical model demonstrated that faster strains can benefit from environments where all food resources are contaminated by toxicants by reproducing in patches that are free of toxicants and resources. In fact, our model predictions were consistent with most of our empirical data except for 000111. Therefore, it is promising that such a model can be applied in some situations, such as in conservation management, to predict effects of heterogeneously distributed toxicants and resources on organisms with different movement strategies.

Previous work has also found that egg retention can promote maternal control over the offspring environment, providing improved offspring protection against environmental stressors (Mignerot et al. 2024). Our present model captures this behavior, which was not accounted for by previous work, and which often assumes that reproduction is proportional to resource level and precludes the possibility of reproduction at a resource-free patch. Furthermore, we also established some theoretical results regarding the dependence of effective growth rates on motility rate, which provided a mechanistic explanation to our empirical findings, such as the higher population abundance observed in strains with higher motility when the distributions of toxicants and resources are completely overlapping (the environment 000333). Other alternative modeling methods may also be applicable; for instance, differential equations incorporating time-delay (Kuang 1993) can also account for the gestation times and transportation time. However, we emphasize that simplistic models such as (1) are not enough to capture the cases where the faster diffuser is selected as observed in the experiments. This work thus adds to the literature regarding modeling organisms with switching behaviors, with the particular emphasis on the separation of the two processes of nutrient uptake and reproduction.

Future directions

The strains used in this study had non-directed movement, meaning that while they were generally attracted by resources and repelled by toxicants, they had defects in both attraction and repulsion. Future studies should focus on whether direct movement towards resources would influence population abundance within these environments. The fast and slow strains were kept on separate plates, so it would be useful to perform competition experiments between them to understand how competition influences their distribution and abundance in these environments. This study mainly focused on the impact of environmental toxicants that created some avoidance behaviors. It is worth noting that our results can be applied to similar avoidance behavior that is caused by fear of predation in the field. Furthermore, this study only used copper as a stressor to cause organismal avoidance, so it would be helpful to use other chemicals that can create different responses to toxicants to create a deeper understanding of these situations. Given that we mainly explored this question using *C. elegans* population abundance data in a Petri dish setting, studies with larger terrestrial species in more complex landscapes would also be useful.

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Author contributions

Ashley Baragary: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Lin Wang**: Data curation (equal); Methodology (equal); Writing – original draft (equal). **King-Yeung Adrian Lam**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Arwa Ali**: Data curation (equal). **Jason Belden**: Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Kevin Collins**: Resources (equal); Writing – review and editing (equal). **Bo Zhang**: Conceptualization (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sxksn03d4 (Baragary et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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